CROSS-SHELF DISTRIBUTION OF SOUTHWEST SULAWESI REEF SPONGES

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Voogd, N.J. de, Soest, R.W.M. van & Hoeksema, B.W. 1999 06 30: Cross-shelf distribution of southwest Sulawesi reef sponges. *Memoirs of the Queensland Museum* 44: 147-154. Brisbane. ISSN 0079-8835.

The quantitative distribution of open reef sponges (number of individuals per square meter) was studied across various reefs in the Spermonde Archipelago, southwest Sulawesi, Indonesia from April-July, 1997. The reefs are situated in 4 shelf zones that vary in distance offshore. Those closest to shore are subjected to freshwater inflow, nutrient input and sedimentation, whereas outer reefs are subjected to wave-action and upwelling from the Makassar Strait. Sponge individuals visible to the eye were identified and counted in 23 $100 \times 1m^2$ belt transects distributed over the four shelf zones at depths of 3m, 6m, 9m and 15m. Distribution patterns of reef sponges were investigated in three spatial scales: 1) distance from land; 2) depth; 3) orientation to wind direction. The highest number of sponge species (richness) and individuals (abundance) was found in a middle-shelf reef, whereas the lowest richness and abundance was found in an inner-shelf reef. Lowest species richness and abundance occur in shallow transects (3-6m), and the highest were found in deeper transects (9-15m). More sheltered sites of reefs are lower in species richness than more exposed sites. Most species appear to have a wide distribution across the Spermonde shelf, and few are restricted to specific reef zones or depths. In contrast, the number of phototrophic sponge species and individuals increases with increasing distance from shore, with the highest numbers in the reefs farthest from shore. The occurrence of these sponges seems to be related to more clear, oligotrophic waters, such as found in the open Makassar Strait. ❒ *Porifera, Spermonde Shelf, Indonesia, sponge distribution, species diversity, phototrophy.*

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Many marine invertebrate species appear to reach their highest diversity in the Indo-Malayan region (Briggs, 1987), and sponges are no exception (Van Soest, 1994). However, sponges in Indonesia have been largely neglected by science for a long time. The few publications on sponges from this area were descriptions of small collections picked up almost casually, published during the first half of the century. Most of our knowledge of the Indonesian sponge fauna is based on collections made by large expeditions, such as the 'Siboga' expedition (1899-1900), and more recently from the Indonesian-Dutch 'Snellius II' expedition (1984-1985). Thousands of specimens were collected and identified, but remained unpublished (Van Soest, 1989). A database of these species, including manuscript names assigned to specimens by the late Maurice Burton (BMNH collections), appear in Hooper et al. (1999). Nevertheless, published information available suggests that a high degree of dissimilarity exists between sponge faunas in various reef locations within Indonesia (Van Soest, 1989; Amir, 1992). Differences in species composition has been mostly attributed to the degree of exposure to waves and currents (Amir, 1992), but these conclusions are based on very few data. Several studies have been made on differences in sponge populations in relation to various physical factors on the Great Barrier Reef. Wilkinson & Cheshire (1989) studied sponge distribution patterns across a broad continental shelf, related to distance offshore and depth. They concluded that highest biomass occurred on inner-shelf reefs and decreased further away from the mainland; abundance was highest on middle-shelf reefs; and this appeared to be correlated with different environmental factors across the continental shelf. Inner-shelf reefs are influenced by terrigenous run-off, high nutrient concentrations and fresh water inflow, whereas outer-shelf reefs are susceptible to oceanic features such as wave energy, oligotrophic conditions and upwelling. Wilkinson & Trott (1985) showed that light was also a factor determining sponge distribution across a continental shelf. Light transmittance varied considerably across a longitudinal continental shelf, and thus influenced the distribution of

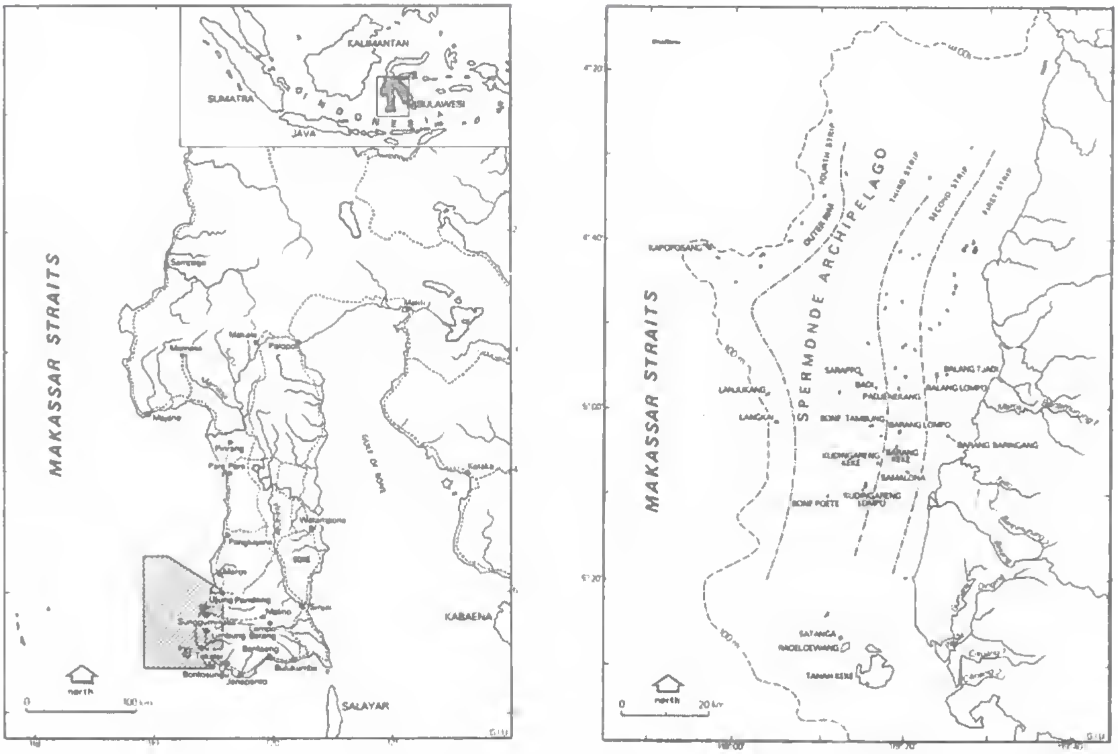

FIG. 1. Location of the Spermonde Archipelago (after de Klerk, 1983). The west side of the archipelago borders the deeper part of the Makassar Strait at the end of the shelf, whereas the east side borders the mainland of Sulawesi.

predominantly phototrophic sponges (i.e. those which rely on translocation of nutrients from cyanobacterial symbionts). Inner-shelf reefs harbour sponges which are primarily heterotrophic, whereas in outer-reefs a larger proportion of sponges are phototrophics (Wilkinson, 1987a). Variation in physical factors such as light, depth and turbulence were suggested as being major factors influencing the local composition of sponge populations across a middle-shelf reef of the central Great Barrier Reef (Wilkinson & Evans, 1989).

The Spermonde Archipelago, SW Sulawesi, is an exception to our otherwise limited knowledge of reefs in the Indo-Malayan region. Extensive marine biological (De Klerk, 1983; Moll, 1983; Hoeksema, 1990; Verheij, 1993) and physical geographic studies (Best & Zonneveld, 1989) have been made in this region, and this presently constitutes one of the better-explored marine regions of Indonesia. It provides a suitable area to conduct a study on distribution patterns of reef sponges similar to those carried out on the Great Barrier Reef, and to test the generality of trends observed by Wilkinson et al. (l.c.). The present paper reports on the distribution of open reef sponges, in relation to potential influences of depth, distance offshore and wind direction.

MATERIALS AND METHODS

The present study was conducted in the Spermonde Shelf off the SW coast of Sulawesi, Indonesia (Fig. 1). The Spermonde Shelf is 40-60km wide and up to 60m deep, and harbours some 150 coral reefs, most cay-crowned. The shelf is divided in four parallel zones (Fig. 2), which vary in distance offshore (Hutchinson, 1945). The study was conducted over a period of 3 months from April to July 1997. Surveys were conducted at four reefs, each located in different shelf zones: an inner-shelf reef, located in the first shelf zone (Lae-lae); middle-shelf reefs, the inner one located in the second shelf zone (Samalona) and the outer one in the third shelf zone (Kudingareng Keke); and an outer-shelf reef located in the fourth shelf zone (Langkai).

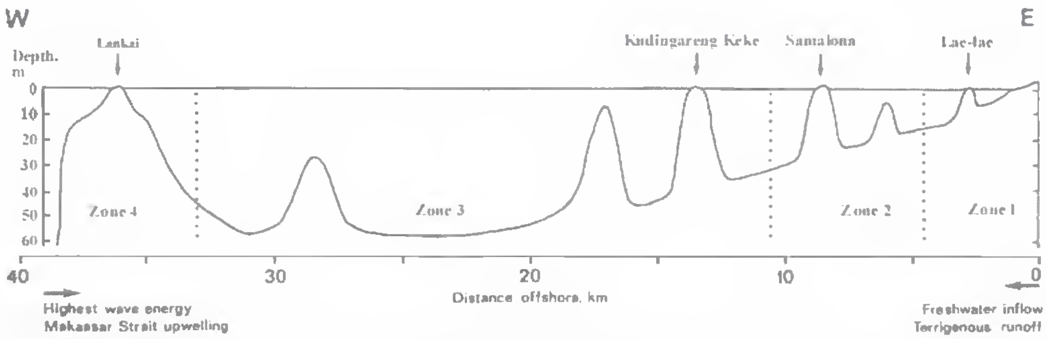

FIG. 2. Schematic cross-section of the Spermonde Shelf (approximately W-E) from Langkai to Ujung Pandang, with the proximate distances from the mainland (after Hoeksema, 1990).

Reefs were surveyed on the exposed side; these are most prone to waves generated by the NW monsoon (November to March). Two reefs (Samalona and Kudingareng Keke) were also surveyed on the sheltered lee side, which is less prone to wave-action. Surveys were conducted at 3, 6, 9 and 15m depth along a 100m transect line. With the aid of a 1m^2 quadrat laid at each consecutive 1m section, sponge species visible to the eye were noted and their numbers counted. Smaller (cryptic, boring and thinly encrusting) specimens were excluded from this study. Representative samples of all sponge species were collected, and after preliminary identification (spicule preparations and hand section) each individual species was given a unique field-code. These samples are currently deposited in the collections of the Zoological Museum, University of Amsterdam (ZMA), where the specimens were identified definitively by the second author (RvS). Six presumed phototrophic sponges were recognised based on their similarities to published descriptions (Bergquist et al., 1988; Wilkinson, 1983, 1987, 1988): *Carteriospongia foliascens, Dysidea aff. herbacea, Halichondria cartilaginea, Phyllospongia papyracea, Phyllospongia* sp. and *Strepsichordaia aliena*. Minimum sampling area was determined by means of the quadrat-area method; whereby the number of species was counted in one m^2. This was repeated after doubling the area, adding species not encountered previously. The number of species was plotted against the area size. Further repetition was undertaken until doubling of the previous area resulted in less than 10% increase in species number (Kaandorp, 1984). In our study, the minimal area was achieved at 64m^2. Since tropical marine ecosystems are far from homogenous, it was considered appropriate to maintain a larger minimal sampling area, 100m^2.

For each transect, sponge species diversity, Shannon-Weaver index H' (Shannon & Weaver, 1949) and evenness index J' (Pielou, 1975) were calculated.

Species composition and relative abundance of species at various reef sites and depths were compared using an agglomerate hierarchical classification based on a (dis-)similarity matrix (CLUSTAN; Wishart, 1978). CLUSTAN was carried out with logarithmically transformed data and the average-linkage method (Sokal & Michener, 1958) in combination with the Bray-Curtis coefficient.

RESULTS

One hundred and fifty-four sponge species were recorded, belonging to 75 genera and 34 families. H' values were found to be in the range of 2.18 (Lae-Lae, 3m depth) to 3.83 (Kudingareng Keke, 15m depth). J' values varied between 0.79-0.92. Twenty-seven sponge species occurred at each of the four reefs ('common species') in the Spermonde Archipelago.

CROSS SHELF DISTRIBUTION PATTERNS. Both the number of species (species richness) and number of individuals (abundance) increased from inshore reefs to the middle-reef region, but further off-shore, at the outer shelf rim, these values decreased. The exposed side of the outer middle-shelf reef at Kudingareng Keke showed the highest species richness and highest abundance averaged over all four depths (Figs 3a, 4a). For each individual depth (transect), the same site also showed the highest species richness. However, the highest abundance of individuals in a transect was observed at the outer-shelf reef of Langkai at 15m (Fig. 4b).

DEPTH DISTRIBUTION. Generally, both species richness and abundance increased with

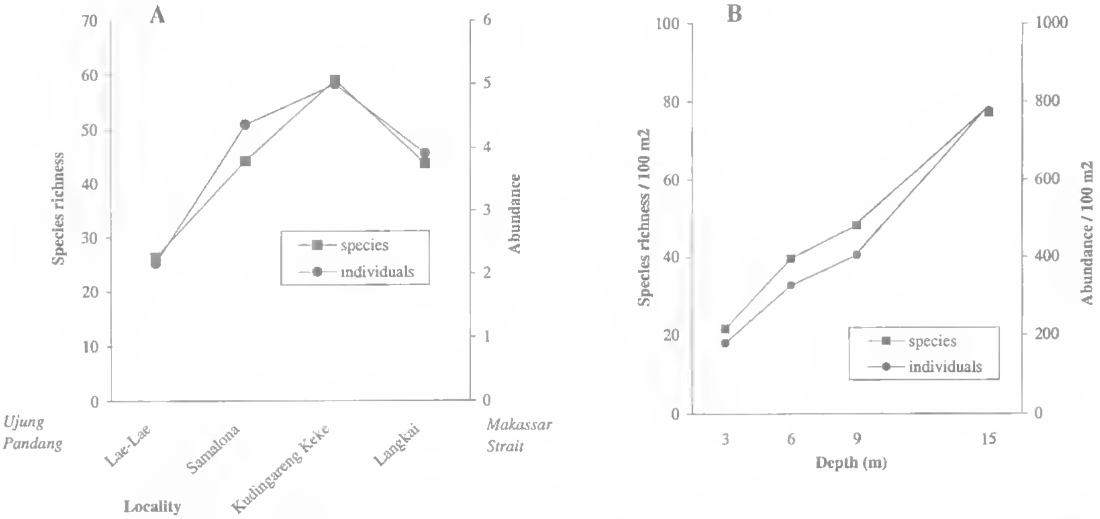

FIG. 3. Species richness (left axis) and abundance (right axis) per reef. A, localities arranged according to distance from the mainland at the capital Ujung Pandang; B, species richness and abundance per depth in metres. Indices are mean values.

increasing depth (Fig. 3b). The situation at the nearshore reef at Lae-Lae differed from that on other reefs (Fig. 4b) in showing a higher richness and abundance at 6m than 9m depths, where the bottom predominantly consisted of sand and silt as compared to hard substratum on other reefs. The 15m depth habitat was absent at Lae-Lae.

EXPOSED VS SHELTERED REEF SITES. Reefs at which both the exposed (west) and sheltered (east) sides were monitored, Samalona (shelf zone 2) and Kudingareng Keke (shelf zone 3), showed the lowest richness and abundance occurring on the sheltered side (Fig. 5). This difference is especially obvious at Kudingareng Keke, where species richness and abundance on the E side are about half that of the W side. Differences in both richness and abundance are most distinct between 9 and 15m depth contours.

PHOTOTROPHIC SPONGE DISTRIBUTION. In contrast to the general trends observed for all sponges, abundance of phototrophic sponges continued to increase with distance offshore (Fig. 6). This trend was also reflected in species abundance, increasing from 2 at the inshore-reef, 4 at both middle-shelf reefs, to 6 at the outer-shelf reef. Conversely, abundance of individual phototrophic species deviated from this trend: *Dysidea* aff. *herbacea* was slightly less abundant at Samalona (middle-shelf reef) than at Lae-Lae (inshore reef), whereas *Halichondria cartilaginea* was slightly more abundant at Kudingkareng Keke (outer middle-shelf reef) than at Langkai (outer-shelf reef). Averaged for all reef locations, the highest abundance of phototrophic species was found at 15m, and of individual transects sampled the highest abundance was found at the 15m transect at the outer-shelf reef of Langkai.

SPONGE COMMUNITY DISTRIBUTION. Similarities in species composition and abundance (number of individuals) of all reef locations and depths were determined by means of cluster analysis (Fig. 7). Three distinct clusters were recognised. Cluster 1 contains all Lae-lae sites. This reef was generally characterised by low species diversity and abundance. The high abundance of *Paratetilla bacca* and *Dysidea* aff. *herbacea* was notable, but these species also occurred elsewhere. Three species were confined to Lae-Lae, but they were rare and represented by only few individuals. Cluster 2 contains all shallow sites of 3m depth, with the exception of Lae-Lae (cluster 1), and is also characterised by low species richness and abundance. Relatively high abundance of *Gelliodes callista, Halichondria cartilaginea* and *Phyllospongia papyracea* were notable, but these also occur in cluster 3. One species is confined to the 3m zone, but only a single individual was found. Cluster 3 comprises the remaining transects. Five species (*Xestospongia ashmorica*, *Haliclona fascigera*, *Niphates olemda*, *Clathria vulpina* and *Ulosa* sp.) meet the criteria to be considered as 'characteristic and dominant species' of this large cluster, occurring in at least 66% of the transects and an average

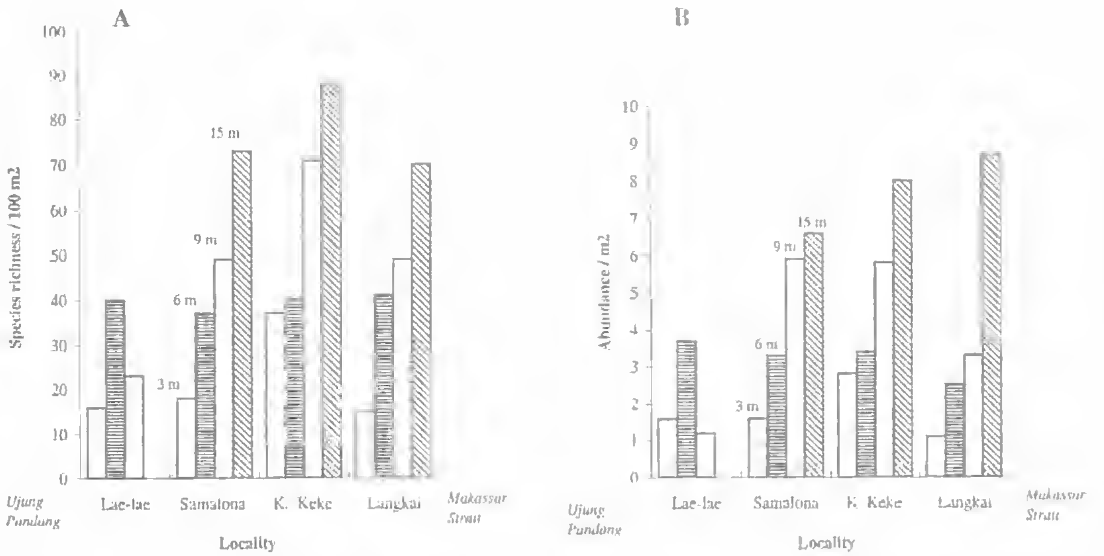

FIG. 4. Species richness (A) and abundance (B) per reef at each depth profile. Each shelf zone is represented by a reef and arranged according to distance from the shoreline at the capital Ujung Pandang.

abundance exceeding 5 % (Kaandorp, 1986). Some species only occur in subsets of this cluster, but their occurrence invariably overlaps only partially with that of other clusters, causing a dissimilarity index too low for confident recognition of distinct clusters. Some patterns are nevertheless worth noting: e.g. all transects on the east side of Kudingareng Keke are grouped together, having in common low species richness and abundance. The dendrogram clearly indicates that the first shelf zone and all the shallow (3m) sites are different from the remaining sites.

DISCUSSION

CROSS-SHELF DISTRIBUTION PATTERNS. Sponge species richness and abundance increase with distance offshore to the third shelf zone, decreasing further offshore. The Spermonde Archipelago is affected by the NW monsoon, both geomorphologically and ecologically (de Klerk, 1983). These differences seem to be related to distance from land, and clearly suggest an environmental gradient across the shelf (Hoeksema, 1990). The lowest number of coral species was found in the outer reef zone, but at the same time the outer-rim high energy environment provides a higher coral cover than on the inner-rim reefs (Moll, 1983). These patterns include all scleractinian corals. A study of cross-shelf distribution patterns in fungiid corals revealed that the number of species increased with increasing distance from shore until the third shelf zone. The fourth reef zone exhibited a lower species richness and abundance. Hoeksema (1990) concluded that the third reef zone was the most optimal reef zone for fungiid species richness. Similar to these trends our results found that the third reef zone was also the most optimal for sponge populations. Moll (1983) found no clear differences in

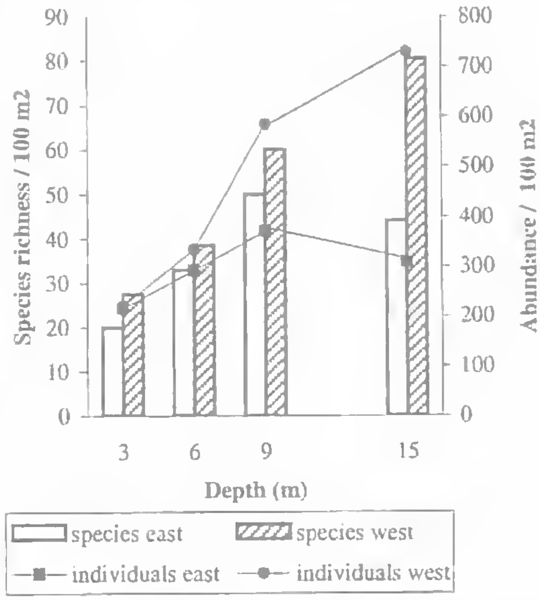

FIG. 5. Species richness (bars: left axis) and abundance (line: right axis). Values are mean values for transects on east and west sides of Samalona and Kudingareng Keke.

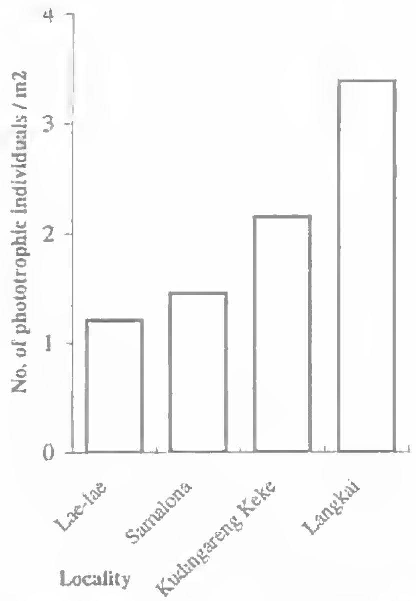

FIG. 6. Numbers of individuals of presumed phototrophic sponges in the four reef areas arranged according to distance offshore.

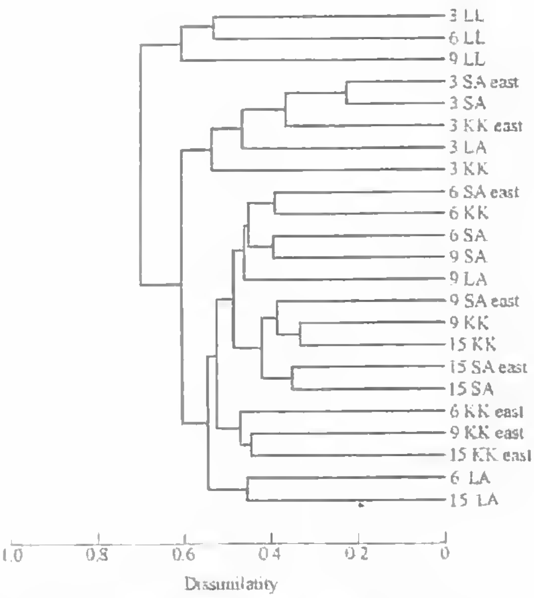

FIG. 7. Dendrogram of a hierarchical classification on species composition and sponge abundance for all transects. Transects are listed with depth in metres. Abbreviations: LL, Lae-lae; SA, Samalona; KK, Kudingareng Keke; LA, Langkai.

scleractinian species richness between reef zones 2 and 3, although the third zone had slightly higher number of species. The largest differences were found between reef zones 2-3 and zone 4. In our study, we found the highest proportion of sponge species with the most restricted distributions occurred at Langkai in the fourth reef zone.

From earlier studies on cross-shelf distribution patterns of sponges on the Great Barrier Reef Wilkinson & Cheshire (1988, 1989) found that sponge biomass showed an inverse relationship with distance from land. They concluded that this was due to high amounts of nutrients in near-shore waters, decreasing with distance from land. Their data correlated with the hypothesis that the clear-water sponge fauna depends predominantly on nutrition from their cyanobacterial symbionts. Abundance of sponges on the Great Barrier Reef was highest in middle-shelf reefs, whereas the pattern of richness appeared more complicated. Sponge abundance on the Spermonde shelf increased similarly with distance from land until the midshelf reefs. Species richness also followed this pattern on Spermonde reefs, whereas this was not the case on the Great Barrier Reef. However, the Great Barrier Reef constitutes a much broader area, with the outer-shelf reefs in the Townsville region located some 200km from land, whereas the inner-shelf reef is almost 20km from shore. Species compositions of Great Barrier Reef zones were not compared between zones, and it is conceivable that distinct faunal assemblages exist over the broad shelf, making ecological comparisons more complicated. The inner-shelf reefs of the Great Barrier Reef are perhaps more comparable with the second and third reef zone in the Spermonde Archipelago, where the inner-shelf reef is located only 1km from urban Ujung Pandang. Presumably, this area is far more prone to terrestrial influences than an inner-shelf reef on the Great Barrier Reef.

Like on the Great Barrier Reef (Wilkinson & Cheshire, 1988; Wilkinson & Evans, 1989), the abundance of presumed phototrophic sponges in the Spermonde area appears to be related to the presence of clear, oligotrophic waters.

DEPTH DISTRIBUTION. On the Great Barrier Reef, high irradiance, high UV light and high wave energy were thought to exclude most species from shallow waters. These factors decrease with increasing depth, hence species richness and abundance increase with depth (Wilkinson & Cheshire, 1988; Wilkinson & Evans, 1989). The depth distribution of sponges at the Spermonde shelf follows this general pattern closely, and it is probable that these mechanisms are also responsible for differential distribution patterns in this region.

WITHIN REEF ZONE VARIATION. Moll (1983) observed that species richness and abundance in scleractinian corals was significantly lower on the E side than at the W side of Spermonde shelf islands. Hoeksema (1990) found that circumreef patterns in fungiid corals were mainly determined by water movement. The W (exposed) side is, in general, the most exposed to wave- energy caused by the strong NW monsoon, whereas the E (sheltered) side shows more sediment accumulation. This was evident from the low species richness and abundance on the E sides of reefs (Hoeksema, 1990). In our study we found that species richness and abundance of sponges are lower on E sides than on W sides of reefs. The slopes of E sides of the islands of Samalona and Kudingareng Keke are very steep and contain high amounts of sediment in comparison with the W side.

In conclusion, most species appear to have a wide range of distribution across the Spermonde Archipelago, and few are restricted to specific zones and depths. However, both species richness and abundance increase with depth, and also with increasing distance offshore until the third reef zone. Specific measurements to correlate with these variations were not made, thus it is not possible at this moment to characterise these habitats.

ACKNOWLEDGEMENTS

The first author received financial support from the Dutch Royal Academy of Science and the STIR-network. We want to thank Universitas Hassanuddin for all help and especially Dr Alfian Noor for the use of his laboratory and all his other support. The research was conducted as part of the WOTRO Programme for Sustainable Management of the Coastal Zone of Sulawesi, Indonesia (W01-60) through grant WK84-354 of the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).

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PERSPECTIVES ON SPONGE-CYANOBACTERIAL SYMBIOSES. *Memoirs of the Queensland Museum 44: 154. 1999*:- Insights on the evolution of sponge-cyanobacterial symbioses are drawn from biogeographic and molecular data. The taxonomic and geographic distribution of sponge-cyanobacteria associations is analysed after surveying their occurrence at eight localities in the Eastern and Western Tropical Pacific, and the Caribbean. Three methods - fluorescent microscopy, thin layer chromatography and transmission electron microscopy - were used to infer the existence of endosymbiotic cyanobacteria.

Thirty-eight species, representing 17 families and 11 orders of Demospongiae, and one family and order of Calcarea, are added to the list of sponges involved in these associations. This number represents an increase of more than 50% over previously known occurrences of this type of metazoan-microbial association. However this increase of species numbers represents only an addition of twelve genera and two families to the taxonomic distribution of these associations. Species from 26 of the 72 recognised Demospongiae families, and 3 of the 17 recognised Calcarea families are found to harbour cyanobacterial endosymbionts. These data suggest a rather restricted taxonomic range for sponge-cyanobacterial assemblages, and invites a search for evolutionary trends among the families involved. The genera with highest number of species harbouring cyanobacteria are: Aplysina (10 spp.), Xestospongia (7 spp.), Dysidea (5 spp.), and Theonella (5 spp.). Although the updated list of sponge-cyanobacterial assemblages shows a few biogeographic trends, the understanding of the evolution of these associations requires the study of more extensive geographic areas.

The use of 16S rDNA analysis to understand the phylogenetic relationships of endosymbiotic cyanobacteria is discussed. Genetic analyses promise to shed light on the understanding of the evolution and specificity of these associations. 16S rDNA gene analyses carried out so far suggest that sponge-cyanobacterial assemblages comprise diverse and complex evolutionary histories, some of which might share evolutionary pathways with other important marine symbiotic assemblages involving cyanobacteria. ☐ *Porifera, cyanobacteria endosymbioses, biogeography, evolutionary trends, 16S ribosomal genes.*

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